




Phytosociology, ecology and conservation status of *Salvia brachyodon* (Lamiaceae), a narrow endemic of Eastern Adriatic

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Ključne besede: CANOCO, ekologija združb, varstvena biologija, Hrvatska, Dalmacija, Črna gora, Orjen, numerične analize.

Abstract

We studied the site ecology of *Salvia brachyodon* (Lamiaceae), a narrow endemic of the eastern Adriatic, which is now restricted to only three sites, using the sigmatistic method and numerical analyses. Four floristically and ecologically well-defined groups of stands, representing different syntaxa, were identified, corresponding to the sampling sites. The majority of stands represent dry eastern (sub)Mediterranean rocky grasslands at different successional stages towards (sub)Mediterranean forest vegetation. Compared to the evolutionary and ecologically closely related and sympatric *S. officinalis*, the morphologically easily distinguishable *S. brachyodon* differs in its flowering phenology and prefers relatively cooler, wetter, deeper and nutrient richer soils, which are developed on dolomite or dolomitic limestone at higher elevated sites. Despite its ability to cope with interspecific competition by means of clonal reproduction better than its congener, the populations are severely threatened by abandonment of traditional land use and by fires, making the species endangered (EN) according to IUCN criteria.

Izvleček

Na podlagi sigmatistične metode in s pomočjo numeričnih analiz smo proučevali ekologijo rastišč kratkozobe kadulje *Salvia brachyodon* (Lamiaceae), ozkega endemita vzhodnega Jadrana omejenega na zgolj tri nahajališča. Ugotovili smo štiri tipe sestojev, ki se floristično in ekološko dobro razlikujejo in se ujemajo z lokacijami rastišč. Večina sestojev pripada suhim vzhodnomediterranskim kamnitim traviščem v različnih sukcesijskih fazah v smeri submediteranskih gozdnih sestojev. Kratkozoba kadulja se od evolucijsko in ekološko ozko sorodnega ter simpatričnega žajblja (*Salvia officinalis*) dobro loči v morfologiji in fenologiji cvetenja, bolje tudi uspeva na relativno svežih, vlažnih, globljih in z nutrienti bogatih tleh na dolomitu ali dolomitiziranem apnencu na večji nadmorski višini. Čeprav se v primjerjavi z žabljem bolj uspešno razmnožuje s kloni, populacije kratkozobe kadulje ogrožajo požari in zaraščanje njenih rastišč vsled opuščanja tradicionalnega gospodarjenja. Skladno s kriteriji IUCN štejemo kratkozobo kaduljo za ogroženo (EN).

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Introduction

Mediterranean biodiversity phenomenon is a result of the kaleidoscopic complexity of past and present topographic, climatic and geological conditions. Although the Mediterranean Basin represents less than 1.5% of the land area of the world, it harbours around 30000 vascular plant species (Blondel et al. 2010, Greuter 1991, Quezél 1985) which represents roughly 10% of all known species of seed plants and ferns on Earth. Besides that, approximately half of Mediterranean vascular plant species are endemics (Gomez-Campo 1985), usually restricted to small areas with specific ecology or geography (e.g., Lavergne et al. 2004), such as more than 5000 islands scattered throughout the Mediterranean Sea (Dallman 1998, Médail & Quezél 1999). Ecologically similar to islands, mountains promote speciation events too, thus harbouring up to 42% of endemic vascular plant species (Médail & Verlaque 1997), which usually consist of a small number of populations and individuals and are thus endangered, if not nearly extinct (Greuter 1991, 1994, Médail & Quezél 1999). Nevertheless, mountain plants often exhibit surprising ability for local survival through perenniality and/or clonality (Bliss 1971). Nowadays, barely 5% of the Mediterranean area covers relatively preserved climazonal vegetation (Blondel et al. 2010; Myers et al. 2000).

Salvia brachyodon Vandas (Lamiaceae) consists of only a few populations in central part of the coastal Dinaric Alps along the eastern Adriatic with small number of individuals. As its name suggests, it has one of the shortest calyx teeth among the sages, but also the longest petals of any European sage. Morphologically it resembles *S. ringens* Sibth. & Sm., a south-east Balkan endemic, which according to the latest phylogenetic research belongs together with *S. officinalis* L. to the *Salvia* s. str. clade (Will & Claßen-Bockhoff 2017). With branched and tall stems as well as large flowers with long pedicels, *S. brachyodon* is easily distinguished from *S. officinalis*. For a detailed morphological description of *S. brachyodon* see Barbalić (1956). In general, the populations of *S. brachyodon* are morphologically rather uniform, although some differentiation between the populations of Sv. Ilija, Pelješac (Croatia) and Podštirovnik, Mt. Orjen (Bosnia and Herzegovina), carried out on a limited character set, was observed (Liber et al. 2014). So far, *S. brachyodon* has only been registered at four localities: (1) Podštirovnik, Mt. Orjen, Bosnia and Herzegovina (Vandas 1889, loc. class.), (2) Mt. Sv. Ilija, Pelješac peninsula, Croatia (E. Brandis in Keller 1915), (3) Velji do, above Konavle, Croatia (confirmed *in situ* recently),

and (4) Mt. Mosor, Croatia (Girometta 1930). The latter (marked with “+” in Figure 1) has not been confirmed *in situ* yet, and there are no vouchers from this locality deposited in herbaria.

So far, a considerable attention from a population genetics point of view received the population of *S. brachyodon* from Mt. Sv. Ilija, where a detailed, high-resolution spatial genetic analysis and a study of the clonal architecture and seedling recruitment strategy identified three large and well-defined and several smaller groups of patches with a total of 14095 shots (Radosavljević et al. 2020). In a previous study at the same site, *S. brachyodon* showed, contrary to expectations, a heterozygote excess and a high level of genetic diversity as well as clonal reproduction and a genetic bottleneck (Radosavljević et al. 2015).

S. brachyodon has a very limited distribution and prefers rocky and open habitats that are nowadays heavily fragmented. To that end, these habitats are under vegetation succession due to abandonment of traditional land use. The population of *S. brachyodon* on the locality Velji do, for example, disappears due to vegetation succession before our eyes. Once much larger, it now consists of only 10 patches (Surina, Glasnović, Balant & Radosavljević, personal observations in 2013, 2015, 2017 and 2019), while population on Mt. Sv. Ilija underwent severe habitat destruction caused by fire in 1999. Although the species is strictly protected in Croatia (Narodne novine 144/2013), is on the Red List in Bosnia and Herzegovina but without designated conservation status (Official Gazette of RS, No. 124/12) and is considered endangered (EN) in Montenegro (Petrović et al. 2008), no active conservation measures have been taken so far. However, in order to propose effective actions, it is essential to have clear understanding of the status of the species in its natural habitat, too (Shaw 2018). Unfortunately, we have only vague knowledge about phytosociology and ecology of *S. brachyodon*, while species' biology is rather unknown. On Mt. Orjen, *S. brachyodon* is usually found on stony pastures and grasslands with shallow calcareous soils, developed on Jurassic dolomitic limestone (Marković 1965, 1975), as well as in fringe vegetation and within thermophytic forests with *Quercus pubescens*, *Carpinus orientalis* and *Fagus sylvatica* (Barbalić 1956). Later, Abadžić and Šilić (1982) documented these stands with seven relevés and ascribed a new association *Lino-Salvietum brachyodoni* Abadžić & Šilić 1982, which they classified into the alliance *Satureion subspicatae* Horvat 1962 and the order *Scorzoneretalia villosae* Horvatić 1975 (*Festuco-Brometea* Br.-Bl. & Tx. 1943). On Mt. Sv. Ilija, *S. brachyodon* is also not limited to stony pastures, but at least in the past it occurred frequently and abundantly on humus-rich soils within the stands of Dalmatian Pine (*Pinus nigra*

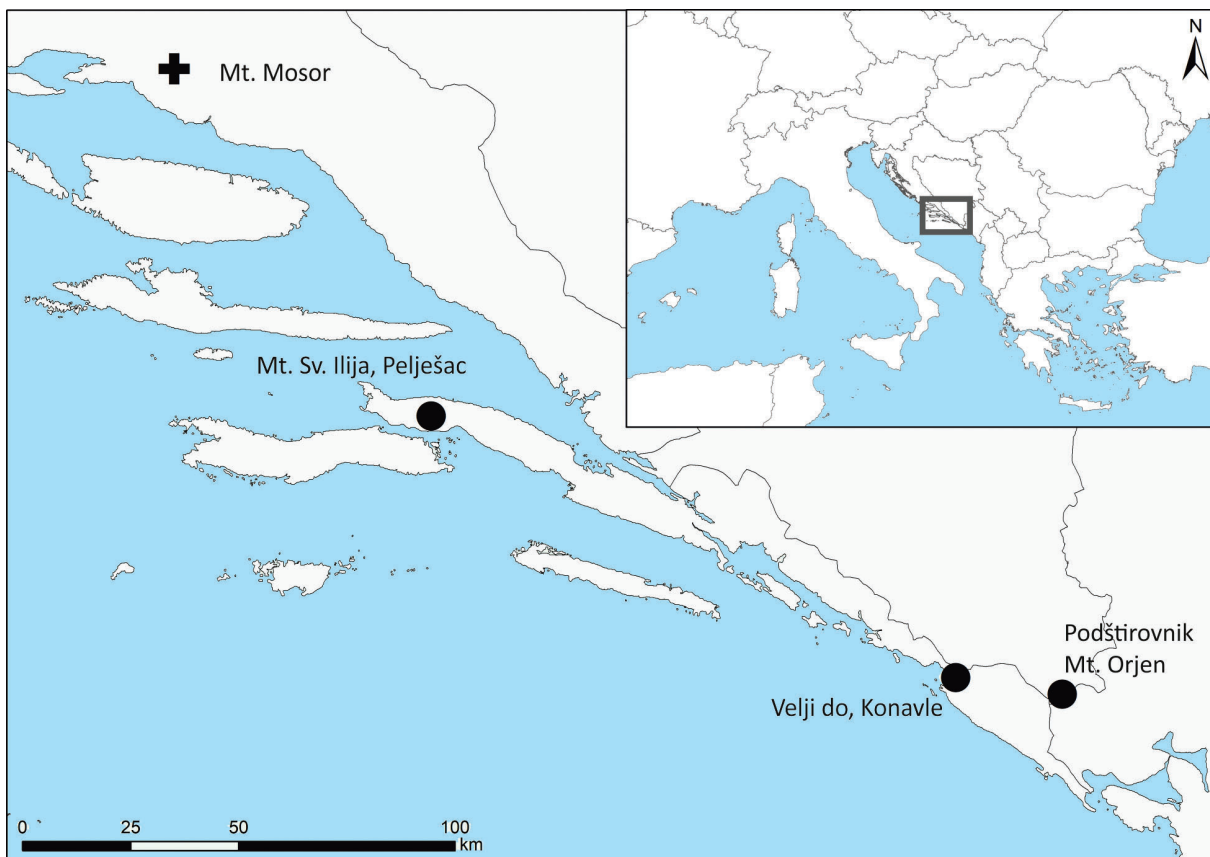


Figure 1: Distribution range of *Salvia brachyodon* Vand. (Lamiaceae).
Slika 1: Območje razširjenosti vrste *Salvia brachyodon* Vand. (Lamiaceae).

subsp. *dalmatica*), developed just above the climazonal evergreen Mediterranean vegetation. These stands with *S. brachyodon* were phytosociologically documented with three relevés by Horvatić (1958), who classified them into the subassociation *Genisto sericeae-Ericetum manipu-liflorae pinetosum dalmaticae* Horvatić 1958 (sub *Genisto-Ericetum verticillatae pinetosum dalmaticae*), alliance *Cisto-Ericion* Horvatić 1958 and order *Cisto-Ericetalia* Horvatić 1958 (*Erico-Cistetea* Trinajstić 1982). Geological bedrock on Mt. Sv. Ilija consists of dolomites and limestones from lower and upper Cretaceous (Korolija et al. 1968; Korolija et al. 1977). According to Marković (1965, 1975), stands in Velji do are developed on Jurassic dolomitic limestones, but their phytosociology and ecology remained unknown. *Salvia brachyodon* often shares sites with morphologically and most likely evolutionarily closely related and much more widely distributed *S. officinalis*, indicating their similar ecological preferences. However, since their flowering phenology does not overlap (*S. officinalis* flowers in spring, while *S. brachyodon* flowers in midsummer), hybridisation between the two species and possible subsequent introgression do not pose

a threat to *S. brachyodon*, as is the case, for example, with *S. fruticosa* (Radosavljević et al. 2019).

This study aims to: (a) fill the gap in phytosociology and ecology of *Salvia brachyodon* and (b) reassess its conservation status. Specifically, we asked: (1) what are the characteristics of its stands and sites? (2) Do the stands differ from site to site, and if so, (3) which environmental/structural factors best explain the variation in floristic composition among the stands? (4) What are the environmental preferences of *S. brachyodon* over the closely related and sympatric *S. officinalis*? (5) What is the extent of occurrence and area of occupancy of the species?

Materials and Methods

Field sampling

We sampled at least 10 relevés (plots of vegetation) per population of *Salvia brachyodon*, 37 relevés in total, by selecting sites with homogeneous plant cover indicating homogeneous ecological conditions within a population area. The cover-abundance estimates for the regis-

tered taxa were made according to a sigmatistic approach (Braun-Blanquet 1928; Dierschke 1994; Westhoff & van der Maarel, 1973), and the relevé size used for sampling was 25 m². To this we added seven relevés with *S. brachyodon* registered by Abadžić and Šilić (1982) on Mt. Orjen. Stands of Sv. Ilija, Pelješac, which were documented with only three relevés (Horvatić 1958), were not included in the analyses. Details of the phytosociological parameters (vegetation cover, stoniness, elevation, inclination and exposition) and the complete floristic inventory of the sites are given in Table 1. The nomenclatural and taxonomic source was Flora Europaea (Tutin et al. 2001).

Species range, population sizes and conservation status

All spatially well-defined patches or individual shots were geocoded using GPS devices and World Geodetic System (WGS84), and all shots, both within patches and individually, were counted for the population on Podštirovnik. For the population on Mt. Sv. Ilija, we adopted data from Radosavljević et al. (2020). The area occupied by the species was defined as the extent of occurrence (EOO) and the area of occupancy (AOO; Gaston 1991). EOO was calculated as the area of the minimum convex polygon (convex hull in the 'Minimum Bounding Geometry' tool). EOO was calculated for each population, we were calculated the minimum convex polygon based on all georeferenced specimens and for the overall present and historic distribution of the species. To estimate AOO, we extracted occurrence data over a 1 km² (1x1 km) grid (Gaston & Fuller, 2009). Density raster was estimated based on the occurrence of singular specimens on Mt. Sv. Ilija (raster resolution 1 m) and in Podštirovnik (raster resolution 10 m) calculating the Kernel densities using number of shots as the population field. All spatial procedures and cartographic representations were obtained using ESRI ArcGIS, ver.10.7. Conservation status of the species was reassessed according to the IUCN Red List categories and criteria (IUCN 2012a) and guidelines for the national level (IUCN 2012b).

Community assemblage data analyses

Prior to numerical analyses, the original cover-abundance values for individual taxa were transformed into the ordinal scale as proposed by van der Maarel (1979). The floristic similarity of studied sites was evaluated using cluster analysis (Wards method and UPGMA, Euclidian distances). Analysis of similarity (ANOSIM) with Euclidian distances (9999 permutations) was used as a non-parametric test of significant differences of relevés among

the localities, where large positive R (up to 1) indicated dissimilarity between groups. Pairwise ANOSIMs (post-hoc) were tested using a Bonferroni corrected *p* values. The significance was computed by permutation of group membership, with 10000 replicates. In order to assess which taxa are primarily responsible for an observed difference between the relevés among the localities, Similarity Percentage (SIMPER) analysis was applied (Clarke 1993) using Bray-Curtis similarity measure (multiplied by 100). Cluster analysis, ANOSIM and SIMPER analyses were performed using PAST version 2.01 programme package (Hammer et al. 2001). To explain the variation in niche assembly by specific environmental and structural (phytosociological) parameters, unconstrained (DCA—discriminant canonical analysis) and constrained (CCA—canonical correspondence analysis) ordination analyses were performed using Canoco v. 5 (Šmilauer & Lepš 2014). To determine the lengths of gradients, DCA analyses, detrended by segments, were initially performed and the models (linear, unimodal) were used accordingly. The statistical significance of the site parameters was tested using the Monte Carlo test with 1000 permutations. To estimate the general environmental affinities of the relevés, indicator values (co-variables) for vascular plants were assigned according to Pignatti (2005) and passively projected into the ordination diagrams. The environmental value in a relevé (EV_w) was estimated as the weighted average of the indicator values of all present species, their abundances being used as weights (Šmilauer & Lepš, 2014). The results of all statistical analyses were deemed significant if the probability of the null hypothesis was less than 0.05. Species response curves for *Salvia brachyodon* and *S. officinalis* on selected environmental parameters were calculated using General Additive Model (GAM), where R provides a measure of explained variation, paralleling the coefficient of determination in classical regression (here calculated as the ratio of the deviance explained by the fitted model and the deviance of a null model multiplied by 100), with F test statistics and following *p* estimate of type I error rate.

Results

Community ecology and species assemblage

In all three sites we registered 144 taxa. Beside *Salvia brachyodon*⁺³, which occurred in all studied stands, *Edraianthus tenuifolius*⁺², *Globularia cordifolia*⁺³, *Genista sylvestris*⁺², *Carex humilis*⁺³, *Genista sericea*⁺⁴, *Teucrium montanum*⁺², *Leontodon crispus*⁺, *Eryngium amethysti-*

num⁺², *Fumana procumbens*⁺¹, *Linum elegans*⁺¹, *Carex kitaibeliana*⁺³ and *Dorycnium germanicum*⁺³ were identified in more than half of relevés (Table 1).

The cluster analysis using the Wards method and Euclidean distances identified four groups of relevés. The same tree topology and groups of relevés were restored by UPGMA analysis (results not shown), while one-way ANOSIM indicated significant differences among the groups (R = 0.8776, p = 0.0001) and between all

group pairs (post-hoc test, Table 2). All main groups of relevés were ranked according to their localities. The biggest differences between the groups identified by SIMPER analysis, were between groups 1 (Mt. Sv. Ilija) and 4 (Podštirovnik) – 85.37% of dissimilarity, while the stands between the two groups of relevés were most similar within the locality of Podštirovnik (groups 3 and 4) – 61.94%, although they differed significantly (Table 2, Figure 2). Group 1 consisted of relevés from Mt. Sv. Ilija, where

Table 2: Multivariate analyses of stands with *Salvia brachyodon* between the localities; first number: One-way ANOSIM (Euclidean distance), pair-wise comparisons with Bonferroni corrected p-values; second number: SIMPER analysis (Bray-Curtis distance) with overall average dissimilarity between stands. Only most important taxa which cumulatively contributed at least 1/3 to the total average dissimilarity are indicated and differential for the group of relevés attributed for the lines. Mt. Sv. Ilija (Pelješac, Croatia), Velji do (Konavle, Croatia), Podštirovnik (Mt. Orjen, Bosnia and Herzegovina) and Podštirovnik (Mt. Orjen, Bosnia and Herzegovina) * correspond to groups of relevés 1–4 in Figure 2, respectively.

Tabela 2: Multivariatna analiza sestojev z vrsto *Salvia brachyodon* med lokalitetami; prva številka: enosmerna ANOSIM (Evklidska razdalja), parna primerjava z Bonferonijevimi popravljenimi p-vrednostmi; druga številka: SIMPER analiza (Bray-Curtisova razdalja) z povprečno različnostjo med sestoji. Prikazani so samo najpomembnejši taksoni, ki skupno prispevajo najmanj 1/3 povprečne različnosti in razlikovalni za skupine popisov Sv. Ilija (Pelješac, Hrvatska), Velji do (Konavle, Hrvatska), Podštirovnik (Orjen, Bosna in Hercegovina) in Podštirovnik (Orjen, Bosna in Hercegovina) * predstavlja skupino popisov 1–4 na sliki 2.

	Podštirovnik Mt. Orjen (12 relevés)	Poštirovnik Mt. Orjen* (12 relevés)	Velji do Konavle (10 relevés)	Mt. Sv. Ilija Pelješac (10 relevés)
Podštirovnik Mt. Orjen (12 relevés)		0.0054 / 61.94% <i>Genista sericea</i> 5.2% <i>Carex kitaibeliana</i> 4.1% <i>Anthyllis aurea</i> 3.8% <i>Sesleria juncifolia</i> 3.0%	0.0006 / 78.76% <i>Linum elegans</i> 6.8% <i>Teucrium montanum</i> 6.3% <i>Carex kitaibeliana</i> 5.5% <i>Anthyllis aurea</i> 4.5% <i>Globularia cordifolia</i> 2.8%	0.0054 / 85.37% <i>Linum elegans</i> 5.8% <i>Genista sericea</i> 4.0% <i>Carex kitaibeliana</i> 3.3% <i>Anthyllis aurea</i> 3.2%
Podštirovnik Mt. Orjen* (12 relevés)	0.0054 / 61.94% <i>Teucrium montanum</i> 8.3% <i>Linum elegans</i> 8.1% <i>Carex humilis</i> 2.9%		0.0012 / 76.51% <i>Globularia cordifolia</i> 4.6% <i>Satureja subspicata</i> 3.2% <i>Plantago holostium</i> 2.5% <i>Linum elegans</i> 2.4% <i>Carex kitaibeliana</i> 2.3% <i>Inula ensifolia</i> 2.1% <i>Anthyllis aurea</i> 1.9%	0.0006 / 74.23% <i>Satureja subspicata</i> 2.6% <i>Globularia cordifolia</i> 2.6% <i>Plantago holostium</i> 2.0% <i>Melica ciliata</i> 2.0% <i>Carex kitaibeliana</i> 1.8%
Velji do Konavle (10 relevés)	0.0006 / 78.76% <i>Bromus erectus</i> 3.6% <i>Quercus pubescens</i> 2.8% <i>Erica manipuliflora</i> 2.7%	0.0012 / 76.51% <i>Genista sericea</i> 3.7% <i>Bromus erectus</i> 3.4% <i>Erica manipuliflora</i> 2.8% <i>Quercus pubescens</i> 2.7% <i>Salvia officinalis</i> 1.9%		0.0006 / 74.83% <i>Genista sericea</i> 3.7% <i>Bromus erectus</i> 3.1% <i>Dorycnium germanicum</i> 3.0% <i>Erica manipuliflora</i> 2.3% <i>Quercus pubescens</i> 2.3%
Mt. Sv. Ilija Pelješac (10 relevés)	0.0054 / 85.37% <i>Teucrium montanum</i> 6.6% <i>Salvia officinalis</i> 5.5% <i>Carex humilis</i> 3.8% <i>Bupleurum karglii</i> 2.6%	0.0006 / 74.23% <i>Salvia officinalis</i> 6.3% <i>Bupleurum karglii</i> 3.0% <i>Satureja cuneifolia</i> 2.7% <i>Euphorbia spinosa</i> 2.5% <i>Carex humilis</i> 2.5% <i>Dorycnium germanicum</i> 2.4% <i>Galium corradifolium</i> 2.3% <i>Teucrium chamaedrys</i> 2.1%	0.0006 / 74.83% <i>Salvia officinalis</i> 4.9% <i>Euphorbia spinosa</i> 3.2% <i>Bupleurum karglii</i> 3.1% <i>Carex humilis</i> 3.0% <i>Koeleria splendens</i> 2.4% <i>Teucrium chamaedrys</i> 2.3%	

*seven relevés retrieved from Abadžić and Šilić (1982)

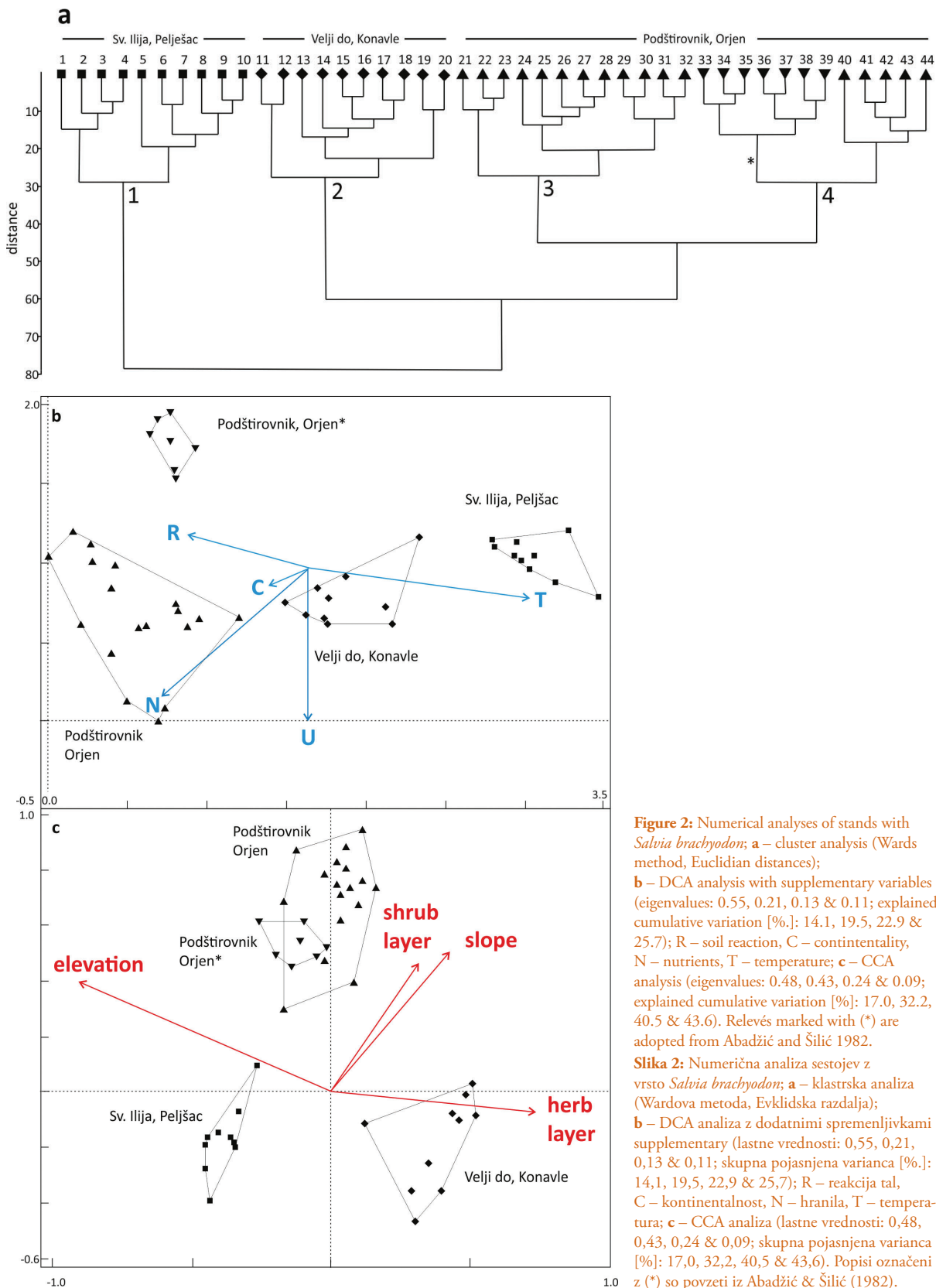


Figure 2: Numerical analyses of stands with *Salvia brachyodon*; **a** – cluster analysis (Wards method, Euclidian distances);

b – DCA analysis with supplementary variables (eigenvalues: 0.55, 0.21, 0.13 & 0.11; explained cumulative variation [%]: 14.1, 19.5, 22.9 & 25.7); R – soil reaction, C – continentality, N – nutrients, T – temperature; **c** – CCA analysis (eigenvalues: 0.48, 0.43, 0.24 & 0.09; explained cumulative variation [%]: 17.0, 32.2, 40.5 & 43.6). Relevés marked with (*) are adopted from Abadžić and Šilić 1982.

Slika 2: Numerična analiza sestojev z vrsto *Salvia brachyodon*; **a** – klastrska analiza (Wardova metoda, Evklidska razdalja); **b** – DCA analiza z dodatnimi spremenljivkami supplementary (lastne vrednosti: 0,55, 0,21, 0,13 & 0,11; skupna pojasnjena varianca [%]: 14,1, 19,5, 22,9 & 25,7); R – reakcija tal, C – kontinentalnost, N – hranila, T – temperatura; **c** – CCA analiza (lastne vrednosti: 0,48, 0,43, 0,24 & 0,09; skupna pojasnjena varianca [%]: 17,0, 32,2, 40,5 & 43,6). Popisi označeni z (*) so povzeti iz Abadžić & Šilić (1982).

79 taxa were recovered. The median (Me) number of taxa per relevé was 37. In these stands dominated *Salvia officinalis*³⁻⁴, while in more than 50% of the samples and/or with high coverage occurred *Carex humilis*¹⁻³, *S. brachyodon*⁺³, *Bromus erectus*¹⁻², *Euphorbia spinosa*⁺², *Koeleria splendens*⁺², *Teucrium montanum*⁺², *T. chamaedrys*⁺² and *Galium corrudifolium*⁺². *Salvia officinalis*, *Bupleurum karglii*⁺² and *Carex humilis*¹⁻³ significantly contributed to the differentiation of group 1 from all other groups. The second well-differentiated group of relevés – group 2 – came from Velji do, where 62 taxa in 10 relevés were recorded (Me taxa/relevé=26). Their averaged dissimilarity ranged from 74.83% (to group 1) to 78.76% (to group 3). The taxa that contributed most to the average dissimilarity across all groups of stands were *Genista sericea*²⁻³, *Salvia brachyodon*¹⁻³, *Erica manipuliflora*⁺³ and *Quercus pubescens*⁺². Groups 3 and 4, which originate from the same area (Podštirovnik), are floristically similar, although they differ significantly. Group 3 consisted of 12 relevés and 59 taxa (Me taxa/relevé=21), and was dominated by *Genista sericea*¹⁻⁴, *Carex kitaibeliana*⁺³, *Anthyllis aurea*⁺³, *Salvia brachyodon*⁺², *Edraianthus tenuifolius*⁺¹ and *Globularia cordifolia*⁺². *Carex kitaibeliana* and *Anthyllis aurea* were differential to all other groups of relevés. In group 4 of 12 relevés we identified 48 taxa (Me taxa/relevé=26), of which *Globularia cordifolia*¹⁻³, *Salvia brachyodon*¹⁻², *Satureja subspicata* subsp. *subspicata*⁺², *Carex kitaibeliana*⁺², *Linum elegans*⁺¹ and *Plantago holosteum*⁺¹ were the most dominant and common. Here *Globularia cordifolia*¹⁻³, *Satureja subspicata* subsp. *subspicata*⁺² and *Carex kitaibeliana*⁺² were differential to stands from groups 1 and 2. Stands from groups 3 and 4 were floristically very similar and differed largely only in coverage and to a lesser extent in the frequency of some taxa; *Genista sericea*¹⁻⁴ (100%), *Carex kitaibeliana*⁺³ (100%), *Anthyllis aurea*⁺³ (100%) and *Sesleria juncifolia*⁺³ (75%) better represented group 3, while *Linum elegans*⁺¹ (100%), *Carex humilis*⁺¹ (92%) and *Teucrium montanum*⁺¹ (75%) were more characteristic of group 4.

Unconstrained analysis (DCA, Figure 2b) also identified four groups of relevés, similar to the cluster analy-

sis (Figure 2a). Supplementary variables accounted for 27.3% of the variation (the adjusted explained variation was 17.7%). The first axis largely corresponded to the gradients of temperature (T) and soil reaction (R), while the second axis corresponded to site humidity (U). Soil nutrients (N) and the floristic composition of the stands explained both axes in a similar way. The stands of group 1 (Mt. Sv. Ilija) seemed to be the most thermophytic, while those of groups 3 and 4 (Podštirovnik) preferred a higher soil reaction. The stands of group 4 (Podštirovnik*) seemed to be less nitrophytic and preferred drier site conditions. The stands of group 2 (Velji do) were located in the middle of the diagram, indicating intermediate site conditions. Constrained analysis (CCA, Figure 2c) and forward selection of environmental factors (Table 3), indicated that elevation explained most of variation (16%; p=0.001), followed by slope (11.5%; p=0.002) and coverage of herb layer (8.7%; p=0.005). Coverage of a shrub layer did not significantly contribute to the explanation of variation (p=0.4895) both within and between samples. Overall, explanatory variables explained 43.6% of the variation (adjusted explained variation was 27.5%). The stands in group 2 were characterized by a significantly higher coverage of a herb layer among all groups of relevés, which was between 45% and 90% of the sampling plots (Me=75%). These stands were also developed at significantly lower elevation (around 490 m a.s.l.) than the other stands (870–910 m a.s.l.). The stands of groups 3 and 4 were developed on more inclined slopes compared to the stands of groups 1 and 2.

Ecological preferences of *S. brachyodon* and *S. officinalis*

Between the two sympatric sages there are clear differences in site preferences (Figure 3). *S. officinalis* prefers drier and more thermophytic habitats at lower elevation. In contrast, *S. brachyodon* is somewhat nitrophytic and prefers relatively humid habitats at higher elevation. It thrives much better in soils with a higher pH reaction than *S. officinalis*. Species response curves of both spe-

Table 3: Forward selection results of the CCA analysis. Total variation is 2.83, explanatory variables account for 43.6% (adjusted explained variation is 27.5%)

Tabela 3: CCA analiza z metodo izbiranja spremenljivk. Skupna variabilnost je 2,83, pojasnjene spremenljivke predstavljajo 43,6% (prilagojena pojasnjena varianca 27,5%).

Environmental factor	Explains (%)	Contribution (%)	pseudo-F	p
Elevation (m)	16.5	37.9	3.4	0.001
Slope (°)	11.5	26.3	2.5	0.002
Herb layer – coverage	8.7	20.0	2.2	0.005
Shrub layer – coverage	6.9	15.8	1.6	0.4895

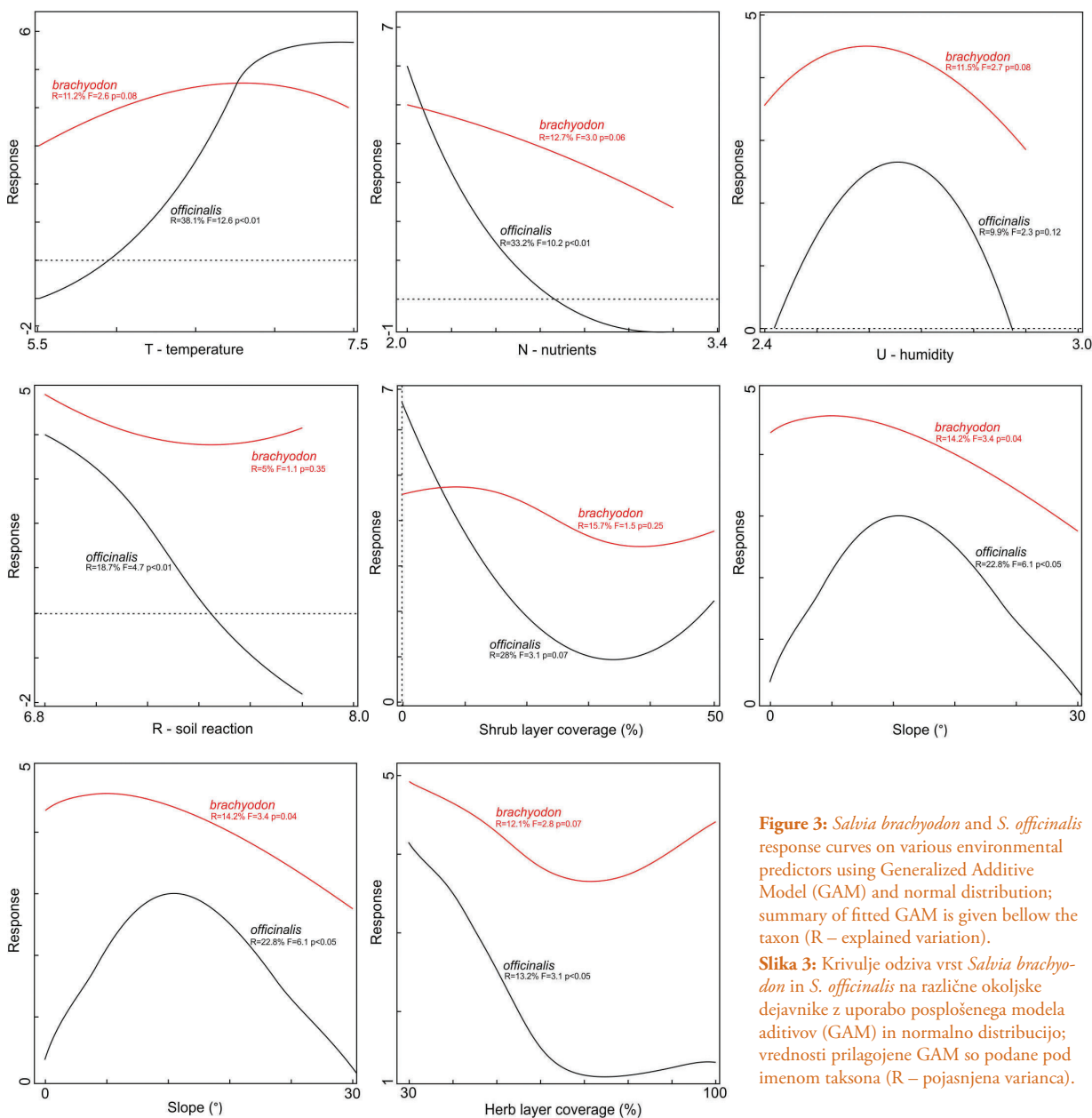


Figure 3: *Salvia brachyodon* and *S. officinalis* response curves on various environmental predictors using Generalized Additive Model (GAM) and normal distribution; summary of fitted GAM is given below the taxon (R – explained variation).

Slika 3: Krivulje odziva vrst *Salvia brachyodon* in *S. officinalis* na različne okoljske dejavnike z uporabo posplošenega modela aditivov (GAM) in normalno distribucijo; vrednosti prilagojene GAM so podane pod imenom taksona (R – pojasnjena varianca).

cies showed that *S. brachyodon* also withstands competition from herbs and shrubs better than its congener. For *S. officinalis* GAM fitted well with several environmental factors, e.g. temperature, soil nutrients and soil reaction, slope, elevation and coverage of the herb layer, whereas for *S. brachyodon* only elevation and slope showed a statistically significant fit to the model, although the p-values for most other factors varied between 0.06 and 0.08. The exceptions were soil reaction ($p=0.35$) and coverage of the shrub layer ($p=0.25$).

Extent of occurrence, area of occupancy and IUCN status

Taking into account three recently confirmed localities (Figure 1), the EOO for *Salvia brachyodon* was 285.6 km² and 2441.9 km² when considering a historical but recently unconfirmed occurrence on Mt. Mosor (Table 4). The largest and most restricted EOOs were recorded at Podštirovnik (355985 m²) and Velji do (4224 m²), while the largest number of shots were recorded at Mt. Sv. Ilija (14095; taken from Radosavljević et al., 2020; Figure 4).

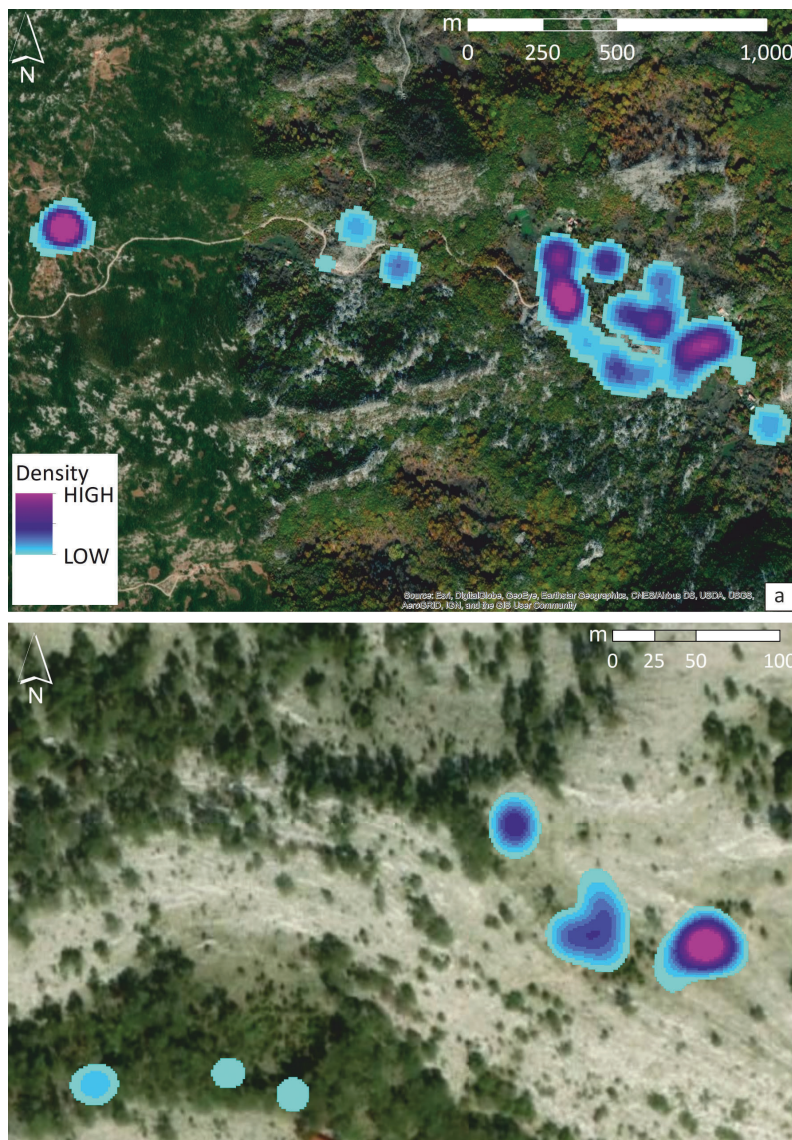


Figure 4: Spatial distribution and Kernel density estimations for the two populations of *Salvia brachyodon*; **a** – Podštirovnik, Mt. Orjen (Bosnia and Herzegovina), **b** – Mt. Sv. Ilija, Pelješac peninsula (Croatia).

Slika 4: Prostorska razširjenost in ocena Kernelove gostote za dve populaciji vrste *Salvia brachyodon*; **a** – Podštirovnik, Orjen (Bosna in Hercegovina), **b** – Sv. Ilija, polotok Pelješac (Hrvaška).

Table 4: Extent of Occurrence (EOO), Area of Occupancy (AOO) and number of shoots of *Salvia brachyodon* on all known localities. For the locality Velji do, only the number of patches is roughly estimated. Mt. Sv. Ilija, Pelješac (Croatia), Velji do, Konavle (Croatia) and Podštirovnik, Mt. Orjen (Bosnia and Herzegovina) correspond to groups of relevés 1, 2 and jointly 3 & 4 in Figure 2, respectively.

Table 4: Obseg pojavljanja (EOO), območje zasedenosti (AOO) in število osebkov vrste *Salvia brachyodon* na vseh znanih lokacijah. Za lokacijo Velji do je število zaplat samo grobo ocenjeno. Sv. Ilija, Pelješac (Hrvaška), Velji do, Konavle (Hrvaška) in Podštirovnik, Orjen (Bosna in Hercegovina) predstavljajo skupine popisov 1, 2 in skupaj 3 in 4 v sliki 2.

Populations	Pelješac Mt. Sv. Ilija	Konavle Velji do	Mt. Orjen Podštirovnik	Total
Extent of Occurrence (EOO, m ²)	16750 m ²	4224 m ²	355985 m ²	285.6 km ² (2441.9 km ^{2*})
Area of Occupancy (AOO, km ²)	1	1	3	5 km ² (6 km ^{2*})
Number of shoots	14095**	10***	11112	?

*taking into account Mt. Mosor; **according to Radosavljević & al. 2020; *** number of patches in 2019.

AOO ranged between 1–3 km², which accounted for the total of 5–6 km² when considering population on Mt. Mosor. The population on Podštirovnik counted 1112 shots. Unfortunately, for the population of Velji do in 2019 we could recover only a maximum of 10 patches of *S. brachyodon* (individual shots were not counted). According to some literature data, specimens of *S. brachyodon* also occur in Montenegro, and some threat assessments and conservation evaluations have even been carried out (e.g. Petrović et al. 2008; Pulević 1983). However, after extensive plant hunting over the border area between Bosnia and Herzegovina and Montenegro, we could not confirm its occurrence in Montenegro.

Considering only the occurrence data, *S. brachyodon* should be classified as endangered (EN) – A1cB1ab(i,iv)+B2a) based on the IUCN criteria v. 3.1. (IUCN, 2012). In addition, when considering changes in population size based on historical distribution data, we can observe a contraction of the range size by about 88%, which meets criterion A1c of an observed decrease in population size $\geq 70\%$ over the last 10 years or three generations. The same conclusion should be reached under criterion B, as the EOO is estimated to be less than 5000 km² and the species thrives in less than five localities (criterion B1), while the AOO covers significantly less than 500 km² (criterion B1).

Discussion

Salvia brachyodon is a (sub)Mediterranean species of open to semi-open, sunny, dry and shallow calcareous rocky grasslands developed within thermophytic deciduous forests of the associations *Aristolochio pallidae-Quercetum pubescentis* and *Seslerio autumnalis-Fagetum* (and their different successional forms). Although the physiognomy of the grasslands appeared to be very similar, the composition of the stands differed considerably and four different groups of stands, which largely corresponded to the sites, could be clearly identified. Stands from Mt. Sv. Ilija, which form the first group (Table 1, rel. 1–10; group 1 in Figure 2), are floristically most diverse and differentiated. Dalmatian pine forests on Mt. Sv. Ilija, documented by four relevés, Horvatić (1958) classified into the subassociation *Genista sericeae-Ericetum manipuliflorae pinetosum dalmaticae*. *Salvia brachyodon* was recorded in three of four relevés, but since these stands have been exposed to severe forest fires and no representative stands with *S. brachyodon* have been recently identified, we have decided not to include them in the analyses. Horvatić (1958) assumed that the stands from Mt. Orjen belong to the same syntaxon despite the absence of an association

edificator and a diagnostic species – *Erica manipuliflora*. However, Abadžić & Šilić (1982) segregated the stands from Mt. Orjen into the then newly described association *Lino-Salvietum brachyodoni* (Table 1, rel. 33–39; 7 of 12 relevés in group 4 in Figure 2). The results of our analyses justified their decision, but since they did not provide a comparative analysis of the newly described association with neighbouring floristically (syntaxonomically) similar syntaxa, its ranking remains to be clarified. It may well belong to some already defined syntaxa from the alliance *Satureion subspicatae* or even to extrazonally developed stands of the alliance *Seslerion juncifoliae* Horvat 1962 (*Seslerietalia juncifoliae* Horvat 1962, *Elyno-Seslerietea* Br.-Bl. 1948). It seemed that stands with *S. brachyodon* from Mt. Sv. Ilija, today most likely belong to a certain form of the association *Stipo eriocauli-Salvietum officinalis* (Horvatić 1956) 1958. In the present paper, however, no attempt was made to name the newly identified groups of syntaxa since this was only possible after extensive comparative analyses. Stands from Mt. Orjen formed two floristically and ecologically different groups of relevés (Table 1, rel. 21–32 and 33–44, respectively; groups 3 and 4 in Figure 2). Although the floristic composition was very similar, the analysis of similarity revealed statistically significant differences ($p=0.0054$), while similarity of permutations accounted for 61.94% of dissimilarity (Table 2). *Genista sericea*, *Carex kitaibeliana*, *Anthyllis aurea* and *Sesleria juncifolia* were differential for group 3 and *Teucrium montanum*, *Linum elegans* and *Carex humilis* for group 4. Results of the DCA analysis (Figure 2b) indicate that stands of the group 3 are developed on relatively deeper, nutrient richer and moister soils. However, these two groups of stands most likely represent two different successional stages of the same association.

Floristically and ecologically, the stands of Velji do (Table 1, rel. 11–20; group 2 in Figure 2) are intermediate between the stands of Mt. Sv. Ilija and Mt. Orjen. They are developed on a somewhat deeper, relatively more nutritious and moist soils with a high coverage of the herb layer. Although they are developed about 400 m lower than the other stands, they are not characterized by a thermophytic herb species assemblage, but rather extensive encroachment of woody species, especially *Quercus pubescens*¹⁻², *Fraxinus ornus*⁺¹ and *Frangula rupestris*⁺¹. These stands, most likely belonging to the alliance *Satureion subspicatae*, today represent a late successional stage to the forests of the association *Aristolochio-Quercetum pubescentis*.

The majority of the accompanying taxa in stands with *S. brachyodon* belong to the Illyrian element, while the presence of e.g. *Linum elegans*, *Genista pulchella*, *Erica manipuliflora*, *Anthyllis aurea*, *Edraianthus tenuifolius*,

Crepis pantoczekii, *Fumana procumbens* and *Globularia cordifolia* indicates that *Salvia brachyodon* prefers soils developed on dolomite or dolomitic limestone. The preference over dolomitic bedrock is also reflected in the analysis, where ecological preferences were compared with *Salvia officinalis* (Figure 3, R–soil reaction). Here the two sympatric congeners showed significant differences in almost all environmental factors tested. It is interesting to observe that strongly clonal *S. brachyodon* is much less susceptible to interspecific competition than *S. officinalis* (Figure 3; covering of herb and shrub layer). In addition, a high degree of intraspecific competition was observed in *S. brachyodon*, too (Radosavljević et al. 2020). It appears that *S. brachyodon* copes better with changes in environmental gradients along different successional stages after abandonment of traditional land use than *S. officinalis*. This characteristic of *S. brachyodon* has already been observed by Horvatić and Barbalić, who noticed that patches of *S. brachyodon* thrive vigorously in gaps of indigenous established and/or degraded forests of *Pinus nigra* subsp. *dalmatica* (Mt. Sv. Ilija) (Barbalić 1956, Horvatić 1958) as well as *Quercus pubescens*, *Carpinus orientalis* and *Fagus sylvatica* (Barbalić 1956).

Historical evidence of the range reduction and its fragmented occurrence in a limited geographical area, renders *S. brachyodon* an endangered (EN) species on the basis of the IUCN criteria. Although the available evidence cannot provide a clear estimate of the number of individuals (genets) per population (a prerequisite for an assessment according to criteria C and D), it is clear that its habitat is seriously threatened by degradation due to wild fires (e.g. Mt. Sv. Ilija, Pelješac peninsula) and the continued succession of vegetation due to abandonment of traditional land use. This is particularly evident in the Velji do (Konavle) population, where only a few patches remain within a highly overgrown habitat by specimens of deciduous woody species.

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